Spatial and seasonal patterns in sighting rate and life-history composition of the white shark Carcharodon carcharias at Mossel Bay, South Africa

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Spatial and seasonal patterns in sighting rate and life-history composition of the white shark *Carcharodon carcharias* at Mossel Bay, South Africa

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White sharks *Carcharodon carcharias* aggregate at specific times of the year at localities along the South African coast. At Mossel Bay, on the southern Cape coast, four sites were sampled (Seal Island, Hartenbos, Kleinbrak and Grootbrak) to investigate spatial and seasonal patterns in relative abundance and life-history composition. These are known aggregation sites within the bay, each having particular physical and/or biological characteristics. Sightings-per-unit-effort data were collected from February to December 2008–2010. Sighting rates demonstrated significant seasonal and interannual variation at the four sites. The highest mean sighting rate was recorded at Seal Island and the lowest at Hartenbos, which might be a consequence of differences in prey availability. The greatest interannual variability was recorded at Kleinbrak, followed by Seal Island, with little variability at Grootbrak and Hartenbos. White sharks appeared to concentrate at Grootbrak and Kleinbrak in summer and autumn, at Seal Island in winter, and at Hartenbos and Seal Island in spring. All life-history stages were present year-round but their occurrence was influenced significantly by season (\(p < 0.05\)), although not site. Few adults (325–424 cm total length) were seen, with the highest frequency being in spring, whereas that of young-of-the-year (≤174 cm) was in autumn. Juveniles (175–324 cm) constituted 78% of the animals sighted, indicating that Mossel Bay is an important aggregation site for this life-history stage.

**Keywords:** adults, Agulhas system, habitat use, juveniles, relative abundance, young-of-the-year

**Introduction**

The white shark *Carcharodon carcharias* is a coastal apex predator that has a circumglobal distribution, occurring largely in temperate systems but also visiting tropical and subtropical waters (Compagno 1997). Its distribution includes South African waters, where it is a protected species (RSA 1998). Specific localities along the South African coast have been identified as aggregation sites, including False Bay, Gans Bay and Mossel Bay in the Western Cape province (Kock and Johnson 2006; Kock et al. 2013; Towner et al. 2013) and Algoa Bay in the Eastern Cape province (Dicken et al. 2013).

The white shark is characterised by a K-selected life-history strategy and thus has a low intrinsic rate of increase, making it particularly susceptible to exploitation (Hoenig and Gruber 1990; Baum et al. 2003). Given its role as a predator, knowledge of top-down effects and degree of interdependency is key to understanding ecosystem functionality (Stevens et al. 2000; Myers et al. 2007; Ferretti et al. 2010). Determination of patterns in temporal occurrence and relative abundance provides insight into the species’ influence on community structure (Ferretti et al. 2010). Such patterns include spatio-temporal habitat preferences or habitat requirements for different sexes and size classes (Heithaus et al. 2007). The insight derived facilitates the effective conservation and management not only of the species but also of the ecosystem of which it is a part (Wirsing et al. 2007; Jorgensen et al. 2010).

The main objective of this study was to identify spatial and seasonal patterns in the relative abundance of white sharks at Mossel Bay. A secondary objective was to define the population structure in terms of life-history stage.

**Material and methods**

**Study area**

Mossel Bay (34°11' S, 22°08' E) is situated centrally within the warm-temperate Agulhas marine bioregion (Lombard et al. 2004) on the southern Cape coast. It is influenced by the southwestward-flowing Agulhas Current that transports warm water from the tropics (Lutjeharms 1998). During summer, coastal upwelling occurs occasionally in the vicinity of Mossel Bay, bringing nutrient-rich waters to the surface (Scott 1951; Schumann et al. 1982). It is a shallow, semi-enclosed bay with a flat bottom composed largely of exposed reef or sand (Johnson et al. 2009). The Hartenbos, Kleinbrak and Grootbrak rivers empty into the bay (Figure 1). Cape St Blaize is a rocky peninsula at the south-western edge. The most notable feature within the bay is Seal Island, a rocky outcrop 800 m from the shore. This island is a protected nature reserve and hosts a colony of Cape fur seals *Arctocephalus pusillus pusillus*, consisting of over 4 000 individuals (Johnson et al. 2009). There were four sampling sites: Seal Island, and the region immediately offshore of the surf zone off the mouths of the...
Hartenbos, Kleinbrak and Grootbrak estuaries, all of which lie above the 15 m isobath (Figure 1). They were selected on the basis of being known aggregation sites for white sharks within the bay (Johnson et al. 2009).

Field sampling
Data were collected at each of the four sites in every month from February to December 2008–2010. A combination of chum and bait was used to attract white sharks to the boat (see Johnson et al. 2009). Once a shark arrived, its total length was estimated by experienced observers when it swam next to a 2 m length of pipe that was attached parallel to the boat. Also, the dorsal fin was photographed for individual identification. Photographs were taken only when the shark was in close proximity to the boat and the dorsal fin was perpendicular to the sea surface. All photographs were uploaded into Adobe Photoshop Lightroom 2 – a photographic cataloguing program. Standardised keywords were applied to the photographs and were used later to filter for potential matches. Keywords indicated the presence of partial amputations (of dorsal, caudal or pectoral fins), black or white pigmentation (dorsal fin), notches (trailing edge of dorsal fin) and artificial tags (acoustic or satellite), and whether the left or right side of the dorsal fin was photographed. Individual sharks were identified and matched using a combination of dorsal fin features (Anderson et al. 2011), namely the notch structure along the trailing edge as well as black or white pigmentation, if present. Identification and matching of individual sharks was performed manually by a single observer.

Data analysis
For each sampling trip, sightings-per-unit-effort (SPUE) was calculated as the number of individual white sharks sighted, divided by the number of hours spent sampling. Because sampling trips occurred both in the morning and in the afternoon, a Student’s t-test was used to test for any significant variation in diurnal activity patterns. SPUE data were analysed using two-way ANOVA, with factors being (a) site and season and (b) site and year, to investigate variation in relative abundance. Seasons were categorised as summer (December–February), autumn (March–May), winter (June–August) and spring (September–November). All assumptions associated with the performance of an ANOVA were met. To determine composition by life-history stage, identified individuals were placed into life-history stages defined by size class: young-of-the-year (YOY; ≤174 cm), juvenile (175–324 cm), and adult (≥325 cm). These size classes approximate those defined in the literature; females mature at c. 450 cm (Francis 1996) and males at c. 360–380 cm (Pratt 1996; Malcolm et al. 2001) and YOY are generally regarded as being 120–150 cm (Francis 1996). Variation in size composition by site and season was assessed using Chi-square ($\chi^2$) and contingency table analysis. To prevent pseudo-replication, only individuals that could be uniquely identified per sampling session were used for the analysis.

Results
In total, 717 sampling trips to the four sites were undertaken (Table 1). Total observation effort was 1 758 h and 20 min, with a mean of 2 h and 49 min per trip. A total of 2 648 white shark sightings were recorded. The highest mean sighting rate of 1.51 ind. h⁻¹ (SD 1.38) was recorded at Seal Island, and the lowest of 0.96 ind. h⁻¹ (SD 1.12) at Hartenbos. The mean sighting rates for the morning and afternoon trips were 1.34 ind. h⁻¹ (SD 1.42) and 1.31 ind. h⁻¹ (SD 1.34), respectively. There was no difference in diurnal activity patterns ($t = 0.26$, df = 692, $p > 0.05$), so the data were pooled for subsequent analysis. Relative abundance at each site was influenced significantly by season ($F_{(6,709)} = 6.1288$, $p < 0.05$; Figure 2). Grootbrak and Kleinbrak exhibited similar seasonal patterns, peaking in summer and autumn. Similarly, Hartenbos and Seal Island exhibited seasonal peaks in spring. Seal Island also exhibited a pronounced winter peak. Year also had a significant influence on relative abundance across sites ($F_{(6,709)} = 7.0631$, $p < 0.05$; Figure 3). Kleinbrak showed a high degree of interannual variation, with the relative abundance decreasing from 2.71 ind. h⁻¹ (SD 2.17) in 2008 to 0.20 ind. h⁻¹ (SD 0.37) in 2010, but there was little variation at the other three sites (Figure 3).

For the analysis of life-history composition, data from 481 sampling trips were used, during which a total of 1 548 sightings were recorded. In all, 261 unique individuals were identified, encompassing a broad size spectrum that ranged from 125 to 424 cm. All life-history stages were present year-round and size composition was influenced significantly by season ($\chi^2 = 31.21$, df = 6, $p < 0.05$; Figure 4). The YOY
(14% of those recorded) sharks peaked in autumn, whereas adults (23%) peaked in spring. Overall, juveniles (78%) dominated the demographic structure of the sharks under study. Site had no significant influence on size composition \( (\chi^2 = 9.32, df = 6, p < 0.05; \text{Figure 5}) \). The YOY sharks contributed the highest percentage at Grootbrak (12%), and adults (18%) the highest at Hartenbos. Similarly, the YOY sharks (5%) were not commonly found at Seal Island and adults (7%) were sighted infrequently at Grootbrak.

**Discussion**

A sound understanding of habitat use is essential for effective population management (Kareiva and Wennergren 1995). Habitat use can be related to three main factors: (i) prey availability, (ii) reproduction and (iii) shelter (Barnett et al. 2010). Prey abundance and movement have been linked to the distribution of sharks (e.g. Sims and Quayle 1998; Sims 2003; Dicken et al. 2006), including white sharks (Ainley et al. 1985; Martin et al. 2005; Kock and Johnson 2006; Dicken and Booth 2013; Kock et al. 2013). In Mossel Bay, given the low number of sexually mature individuals and YOY, reproduction seems unlikely to be a driving force associated with habitat use.

Seal Island had the highest mean sighting rate of white sharks, followed by Grootbrak, Kleinbrak and lastly Hartenbos. White sharks frequently prey on Cape fur seals at rookeries off southern Africa and particularly so during winter, when juvenile seals leave to forage offshore for the first time, rendering them vulnerable to predation by white sharks (e.g. Martin et al. 2005; Hammerschlag et al. 2006; Kirkman et al. 2006). Similarly, Ainley et al. (1981, 1985) observed that white shark occurrence coincided with the presence of juvenile northern elephant seals *Mirounga angustirostris* at the South Farallon Islands, USA. Cape fur seals have been shown to be targeted by white sharks in the vicinity of Seal Island (Johnson et al. 2009). Hartenbos lies just to the north of the hunting grounds and is generally used as a resting
area for white sharks (Johnson et al. 2009). Hence the low sighting rate there is likely to be due to sharks being less active than at other sites. The Kleinbrak and Grootbrak study sites are characterised both by reef systems and by estuary mouths, with the mouths representing typical nursery areas for a number of estuarine-dependent marine fish species (Houde and Rutherford 1993; James and Harrison 2008). The large biomass of fish present at these sites (James and Harrison 2008) represents potential non-mammal prey. The second lowest sighting rate of white sharks was recorded at Kleinbrak, where fish are less abundant than at Grootbrak (James and Harrison 2008). Seasonal shifts in prey abundance may cause white sharks to switch their diet between marine mammals (e.g. pinnipeds) and demersal teleost or chondrichthyan species (Martin et al. 2005; Bruce et al. 2006). Through such feeding activities white sharks potentially play a large role in influencing ecosystem dynamics through direct and indirect predation effects (Stevens et al. 2000; Heithaus et al. 2002; Myers et al. 2007), supporting the suggestion of Ferretti et al. (2010) that predators utilising large areas are important because they usually prey on multiple species in different systems and/or habitats. This was observed in the present study in which sighting rates for white sharks were high at Seal Island in the winter and at Kleinbrak and Grootbrak in the summer.

Only sharks larger than 300 cm are considered capable of consuming large marine mammals such as seals (Tricas and McCosker 1984; Klimley 1985; McCosker 1986; Cliff et al. 1989; Estrada et al. 2006). Hartenbos is near to Seal Island and hence the presence of seals at Seal Island may explain why these two sites host the greatest proportion of adult sharks. In Spencer Gulf, South Australia, Strong et al. (1996) found that small white sharks appeared to limit their spatial use to reduce direct interactions with larger conspecifics. This may explain why Grootbrak, the farthest site in terms of proximity to Seal Island, had the highest sighting rate of YOY sharks. Surprisingly, however, Seal Island had the second highest sighting rate of YOY sharks. Life-history stages were significantly influenced by season and not site, and hence the rocky reefs of Seal Island may attract YOY sharks when adult sharks are not present.

Mossel Bay provides sheltered conditions throughout most of the year (Jewell et al. 2013) and hosts a diverse array of prey species that collectively represent potential prey for all life-history stages of white sharks (James and Harrison 2008; Johnson et al. 2009). However, despite the wide size range of sharks observed in our study (124–424 cm), a large proportion (78%) were between 175 and 324 cm, suggesting preferential use of the bay by juveniles. The size composition of white sharks on the South African coastline appears to increase from east to west. Algoa Bay (33°50'S, 26°17'E) seems to host the greatest proportion of YOY sharks, Gans Bay (34°68'S, 17°41'E) hosts a similar size composition to Mossel Bay – although with a greater proportion of subadult – and the greatest proportion of adults is found in False Bay (34°04'–34°23'S, 18°26'–18°51'E) (Kock and Johnson 2006; Dicken et al. 2013; Towner et al. 2013).

Our study provides information on the relative abundance and seasonal and spatial distribution of different life-history stages of white sharks within Mossel Bay, and identifies some factors that potentially explain the observed patterns. In addition, it demonstrates the importance of Mossel Bay as an aggregation site for juvenile white sharks, in particular. This provides a basis for ensuring that the ecosystem health of the bay is maintained, as part of the network of aggregation sites for this protected species.

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